

Brains, grouping and language

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Robin Dunbar has suggested two original and stimulating ideas about limits to group size and the origins of language. First, brain size limits the number of relationships that primates can monitor, and therefore limits group size. Second, language did not start with males talking about the hunting environment but with females talking to, and about, each other in order to cement friendly social relationships.

Dunbar opens his target article with the statement that primates are the most social of animals, and continues with the proposition that large brains and consequent intelligence evolved for processing information about the social rather than the physical environment. His argument depends crucially on these precepts. But what is meant by "social" in this context, and what evidence is there that the large-brained primates are using their extra processing ability for social ends? After all, a number of nonprimates live in large, stable, social groups with multiple levels of different sorts of social relationships (Moss & Poole 1983).

Primates certainly are socially complex (Byrne & Whiten 1988; Cheney & Seyfarth 1990; Harcourt & de Waal 1992), but until recently statements that they were more complex than nonprimates were almost entirely unsubstantiated. However, it seems that primates might form uniquely complex alliances (de Waal 1992; Harcourt 1992; Wrangham 1983), as might some members of that other big-brained taxon, the toothed whales (Connor et al. 1992). Thus, only primates are known to cultivate actively alliances with others (by grooming them, for instance) on the basis of differences among those others in their ability or readiness to give useful help, such as during fights (Harcourt 1992).

Dunbar supported his contention about the importance of social intelligence and the constraint that information-processing ability imposed on group size with the observation that the size of the neocortex correlated with group size. However, both brain size and group size correlate with how animals use the environment: primates that rely largely on fruit have larger brains than do the leaf-eaters and they also live in larger groups (Clutton-Brock & Harvey 1977a; Sawaguchi 1990). And, of course, resource patches are not infinitely large. Is social intelligence separable from environmental intelligence as a selective force, therefore? And is brain size or resource-patch size the limiting factor on group size?

It is easy to see how environmental and social intelligence would be necessarily linked and logically very difficult to separate. Larger resources are rarer and more widespread, and so more difficult to find (Milton 1988). At the same time, larger resources allow larger groups, which mean a greater number of competitive and cooperative relationships to monitor and service. That having been said, improved ability at complex manipulation of the social environment by one animal cooperating with others for its own or its relatives' competitive benefit will cause a process of positive feedback, as other members of the social environment respond, that presumably proceeds at a far greater rate than can result from interaction with the physical environment (Harcourt 1992).

Turning to limitations on group size, abundant observational and experimental evidence shows that one constraint is the size of the resource patch that group members can simultaneously use. Another constraint is the time available for the social interactions maintaining the bonds between individuals that cause the group to cohere, which is determined by availability of resources (Dunbar 1992b). Now Dunbar appears to argue that ability to monitor relationships, rather than service them, is the ultimate limiting factor. I do not see how that can be the case,

but we can test the idea more directly by discovering how often individuals have time to service as many relationships as they can monitor, which in turn depends on how many more they can monitor than service.

I know of only one study designed to test limits to primates' knowledge of group members. Mori (1977) found that in groups of less than 300 animals, individuals were confident about whether or not to attempt to obtain a peanut thrown between them and another monkey, as if they knew not only the identity of the other but also their relative competitive ability; above that group size, they were hesitant. Three hundred is much higher than Dunbar's postulated maximum group size for any primate. Admittedly, the knowledge tested by Mori is relatively simple. At the same time, the fact that fairly stable groups of several hundred macaques were available for Mori's study appears to be strong evidence against Dunbar's hypothesis.

The crux of Dunbar's second main hypothesis, about the origins of language, is that language functions in the same way we think grooming does, namely, to cement, and perhaps monitor, social bonds (i.e., cooperative relationships) between group members. The reason grooming functions in this way is that it is potentially useful to the recipient who, the argument goes, later reciprocates the service (Cheney & Seyfarth 1990). Much communication is potentially useful to the recipient, some so useful that animals are punished if they do not communicate (Hauser 1992c), but is there any evidence that vocalizing enhances social bonds in the way Dunbar suggests?

Directedness is a crucial feature of arguments about the origins of reciprocally cooperative relationships because these can evolve only if donors distinguish those who reciprocate from those who do not, and continue to service only the former (Axelrod & Dion 1989; Boyd 1992). Whereas grooming is manifestly directed, vocalizations are less obviously so. However, if prairie dogs are more likely to give alarm calls in the presence of close relatives (Hoogland 1983), the potential is there. Furthermore, monkeys can vocally communicate information about their relationships, giving different screams depending on the identity of opponents (Gouzoules et al. 1984). But, can animals communicate nonverbally about others' relationships, or does that ability arise only after language has evolved?

The functions of grooming and language: The present need not reflect the past

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Chomsky has argued that human language is possible because we are equipped with a piece of neural machinery that permits complex combinatorial manipulations of grammatical structures. From Chomsky's perspective, the communicative function of language is purely accidental. Robin Dunbar's provocative hypothesis contrasts with the Chomskian view by arguing that language is an adaptation, its function being to service the complexities of our social lives. In this commentary we begin by pointing out two theoretical problems with Dunbar's hypothesis. We then discuss issues where additional data are needed and conclude with some comments on how several of Dunbar's statements may be inconsistent with published data.

Current function need not reflect initial function, especially given changes in the environment that shape the adaptive landscape. Dunbar explicitly states "that language evolved as a 'cheap' form of social grooming, thereby enabling the ancestral humans to maintain the cohesion of the unusually large groups demanded by the particular conditions they faced at the time"

(sect 3.2, last para.). Given the data presented, we agree that a powerful function of language is to service a large number of complex social relationships. This does not, however, entail evidence that language evolved *in order to* service such relationships. Dunbar's hypothesis is best seen as an explanation for one of the many functions of language in modern humans (i.e., current function) and not an explanation for why language evolved (i.e., origins), whenever it did.

Our second conceptual problem with Dunbar's hypothesis concerns the function of grooming. We disagree with the basic premise that grooming functions to maintain group cohesion. Although time spent grooming may increase with group size, and although there is sufficient evidence to argue that grooming maintains and builds social bonds, there is no evidence to suggest that primates groom more individuals or groom in a more egalitarian way as group size increases (Cheney 1992). In other words, there is no evidence to suggest that primates are forced to increase the size of their social networks as group size increases. Many other explanations could be given for the relationship between group size and time spent grooming. Therefore, there is no reason to argue that a new mechanism was needed to service more relationships in a more efficient manner.

Even if it were possible to demonstrate that grooming functions to maintain group cohesion, we see two related problems with Dunbar's hypothesis. First, language may not be a good substitute for grooming as a bond-servicing mechanism because of the differential costs involved in the two behaviors. Grooming may function to strengthen bonds (between certain individuals) precisely because it is costly to produce and thus reliably signals the groomer's intent to invest in the relationship. In contrast, language is a relatively cheap form of investment, making it more difficult for the receiver to detect cheaters. Second, because Dunbar never defines what he means by a "relationship," it is difficult to assess why big brains and language are necessary for servicing a relatively large network of social interactions. Intuitively, it seems clear that some relationships are more costly to service than others. For example, factors such as loyalty and kinship are likely to make relationships relatively cheap, whereas power relationships such as those that exist between bosses and employee are likely to be more costly. Consequently, future empirical tests of Dunbar's hypothesis will first require a more rigorous depiction of the quality/nature of each relationship so that a more accurate discussion of cognitive demands can be evaluated. This is important because an individual with 200 "relationships" may be able to add on additional ones because a large proportion of the current relationships is cost-free. The possibility of a cost index for social relationships may allow us to explain more properly why the relatively small-brained black and white colobus monkey can live in groups of up to 200 individuals whereas the relatively large-brained orangutan is solitary.

In attempting to follow the logic of the theory presented there were a number of places where we were unsatisfied with the level of detail. We would very much like to hear Dunbar's thoughts on the following comments: (1) He considers neocortex ratio to be the most important neural structure for keeping track of complex social relationships. Why the neocortex? If memory is crucial, why not look at the hippocampus or the prefrontal cortex? Evolutionarily, one of the major differences in comparative neuroanatomy between humans and all other vertebrates lies in the prefrontal cortex. Goldman-Rakic (1988) and others have pointed out that the prefrontal cortex is the primary center for working memory and is thus likely to play a critical role in the dynamics of an individual's social environment. The hippocampus is likely to be critical for long-term storage of information. (2) By excluding fission-fusion societies, Dunbar has ignored what is socially and cognitively one of the most complex primate species: the chimpanzee. Where do chimpanzees and the other apes fit on the neocortex-ratio group-size regression?

In addition, humans are often depicted as a fission-fusion species (e.g., Rodseth et al. 1991), which gives added justification for including fission-fusion species into the analysis. (3) Even if grooming could be argued to be an important factor in social cohesion, it is surely not the only factor. Is it possible to perform a multivariate analysis of grooming as well as other factors, such as the distribution of resources, to look at the relative contribution of each while holding the others constant?

Finally, there are four statements we believe are inaccurate. First, Dunbar defends his use of mean group size as the relevant variable for comparison by claiming that fissioning occurs when group size reaches a maximum and thus represents a size beyond the hypothesized cognitive constraints. This generalization is based on a few genera (e.g., Catarrhinae) and does not reflect the demographic patterns of other species in his sample (e.g., *Alouatta*, *Gorilla*), which show fluctuations in group size due to individual dispersal rather than group fission. Since the mean is highly vulnerable to extremes (such as newly formed groups), we suggest that the maximum group size represents a more accurate estimate of cognitive constraints on group size. Second, Dunbar's calculation of human group size is distorted by his underestimates of prosimian social network size (Bearder 1987); and, we believe, inappropriate log-log transformations. If one uses data on prosimian sleeping group size rather than foraging group size, the regression equation predicts a human mean group size of 71.5 (log-transformed data) or 58 (raw data). This predicted group size does not coincide with the empirical data reported by Dunbar. Third, it is stated that the only paper on the phonetic structure of primate contact calls is Richman's (1978; 1987) work on gelada baboons. There are several studies on species such as rhesus monkeys and vervet monkeys showing formantlike patterns (Owren & Bernacki 1988), prosodic contours (Hauser & Fowler 1991), and nasality (Hauser 1992a). These are all important features of human speech. Fourth, Dunbar claims that the conversational structure of geladas is unique. Not only have other studies provided evidence of conversations among group members, but they have documented more convincingly than Richman both the mechanisms underlying conversational turn-taking (Hauser 1992b) and the social function of conversations (reviewed in Snowdon 1990).

In summary, Dunbar has presented some intriguing ideas on how brain size may constrain social complexity and how different behavioral mechanisms have evolved to deal with the intricacies of primate social relationships. Although language is clearly used to service our social relationships, it is also used for several other functions. Reconstructing the original function of language is likely to remain a highly speculative endeavor.

Another primate brain fiction: Brain (cortex) weight and homogeneity

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Dunbar's is a very interesting hypothesis that carries much further some speculations I once made regarding the link between neural and behavioral complexities (Holloway 1967; 1981), which I still believe evolved in a positive feedback relationship. The suggestion that language might be viewed as a "cheap" form of social grooming is particularly fascinating, and Dunbar deserves a lot of credit for bringing together so many seemingly disparate elements. My comments must be brief, so I will limit them essentially to the role of the neocortex in language and its relation to other measures such as encephalization coefficients, extra cortical numbers, and the like, even though I suspect that many critical questions should be aimed at